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Monophyly of the Myriapoda? Reliability of current arguments

by

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ABSTRACT

Current support for myriapod monophyly is revised based on a comparative study of the head morphology in Tetramerocerata (Pauropoda) and Pselaphognatha (Diplopoda). New data on the cephalic endoskeleton permit a reconstruction of the common pattern of the myriapod 'tentorium'. *Polyxenus lagurus* (Pselaphognatha) shows no principle difference to the original state in the Chilognatha (Diplopoda). The state in *Pauropus* sp. (Tetramerocerata) also corresponds to the common pattern employed in this study. The composite nature of the 'fulturae' is emphasised, which renders this term inappropriate for outgroup comparisons. The homology of the tentorial components in myriapods is confirmed. The mobility of the tentorium is specified to be mainly based on the presence of its 'transverse bar' serving as an attachment site for the muscles that effect the forward swing of the tentorium. The manner of how the tentorial swing is translated into movements of the primarily moveably separated gnathal lobe of the mandibles, differs in the Dignatha (Pauropoda + Diplopoda) from the state in the Symphyla and Chilopoda. Tentorial mobility seems to be maintained in the Tetramerocerata, despite the fact that the mandibular gnathal lobe is no longer moveably separated from the mandible base in this group. Available data tend to favour myriapod monophyly, not only under the Pancrustacea, but also under the Tracheata hypothesis. Reserve, however, is justified due to corresponding character states in Geophilomorpha (Chilopoda) and 'Entognatha' (Hexapoda). Collembola in particular indicate that the mandibular gnathal lobe in hexapods may be secondarily fused with the mandible base. Final decisions require clarification of the origin and homology of the mandibular and tentorial muscles.

INTRODUCTION

The long-standing debate on the monophyly of the Myriapoda (Chilopoda + Progoneata) is primarily due to the traditional assumption that their closest relatives within the arthropods are the insects (Hexapoda) (e.g. Dohle 1980; Kraus & Kraus 1994). Based on this assumption, quite different views on the inter-relationships between the myriapod subgroups and the insects were expressed (for review see Giribet *et al.* 1999). Among these, a sister-group relationship between Progoneata and Hexapoda is still repeatedly favoured over a monophyletic Myriapoda (see e.g., Kraus 1998 2001 *versus* Ax 2000). The existence of a clade composed exclusively of Chilopoda, Progoneata and Hexapoda (Tracheata- or Atelocerata-concept), however, is no longer supported by recent cladistic analyses (Zrzavy *et al.* 1998; Giribet *et al.* 2001). A considerable number of arguments derived both from morphological and molecular analyses favour the view that insects form a monophyletic group with crustaceans, with myriapods excluded (Pancrustacea- or Tetraconata-concept; for review see e.g., Dohle 2001; Friedrich & Tautz 2001; Hwang *et al.* 2001). According to this view, doubts on the monophyly of the Myriapoda are no longer justified. Support for a monophyletic Myriapoda, however, is weak (see e.g., Edgecombe *et al.* 2000; Giribet & Ribera 2000). Current evidence mainly comes from molecular data (Regier & Shultz 2002; Kusche *et al.* 2002). Morphology, in contrast, was considered to reveal 'no positive character (…) in favour of the Myriapoda' (Dohle 1998: 309), only some shared reductive traits. Recently, however, Kluge (1999) as well as Edgecombe & Giribet (2002) reinforced arguments that Manton (1964) and Boudreaux (1979) had already put forth in support of the monophyly of the Myriapoda. Characters in concern all relate to peculiarities in mandible structure and mechanics. In order to test their alleged phylogenetic significance, the head morphology in Tetramerocerata (Pauropoda) and Pselaphognatha (Diplopoda) have been reinvestigated. In this paper, the first results on the cephalic endoskeleton are presented. They permit a revision of current claims that morphology provides reliable arguments in favour of myriapod monophyly.

MATERIAL AND METHODS

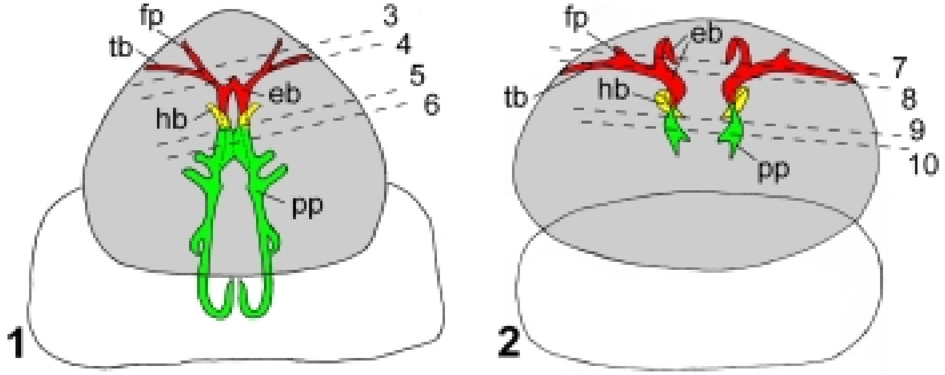
Juvenile and adult specimens of *Pauropus* sp. (Pauropoda) from the Teutoburger Wald (near Bielefeld, Germany) and *Polyxenus lagurus* (Diplopoda) from the Mediterranean coast at Banyuls-sur-Mer (France) were used for this study. For light microscopy (whole mounts), specimens were fixed in ethanol (70 %) and macerated in a solution of pepsin (according to Hilken 1994). Chitinous parts were stained with chlorazol black (Goto 1964), embedded on slides in Hoyer's mixture (Kraus 1984), and examined with an Olympus BX 50 light microscope by interference contrast. Hexapod juveniles (postembryonic stadium I) were used for reconstructions of the cephalic endoskeleton from complete serial sections. For this purpose, specimens were covered with a droplet of absolute alcohol and then immediately fixed with 2.5 % glutaraldehyd buffered in 0.1M sodium cacodylate for 1h at 4 °C. Ruthenium red was added to the primary fixative. Postfixation was performed with 1 % OsO_4 buffered in 0.1M sodium cacodylate for 1 hour at 4 °C. Specimens were dehydrated in an acetone series, embedded in Araldite and sectioned with diamond knifes on an Ultracut E microtome (Fa. Reichert). Series of ultrathin, silver interference coloured sections were mounted on formvar-covered single-slot copper grids, automatically stained with uranyl acetate and lead citrate (LKB Ultrostainer), and examined with Hitachi H500 and Phillips CM 100 electron microscopes. Series of semithin sections were stained with 1 % Toluidin (modified according to Trump *et al.* 1961) and examined with an Olympus BX 50 light microscope.

RESULTS

As deduced from the present light microscopical studies, juvenile and adult specimens show no principle difference in the structure of the cuticular cephalic endoskeleton. The following description is restricted to the 'tentorium'. This formation comprises paired endoskeletal rods connected with paired exoskeletal bars extending along the roof (epipharynx) and the bottom (hypopharynx) of the preoral chamber. Available descriptions of this formation in the Lithobiomorpha (Chilopoda) (Snodgrass 1951; Applegarth 1952; Manton 1965; Desbalmes 1992) serve as a reference (cf. Fig. 11). Only the major differences in *Pauropus* and *Polyxenus* are pointed out in the following description. Complete three dimensional reconstructions, including musculature, are still in preparation.

Pauropus sp.

The tentorial complex in *Pauropus* sp. (Fig. 1) comprises the same components as in the Lithobiomorpha. Paired rod-like processes (*pp*) similarly arise within the preoral chamber on each side of the mouth (= opening of the pharynx; Fig. 5) and extend

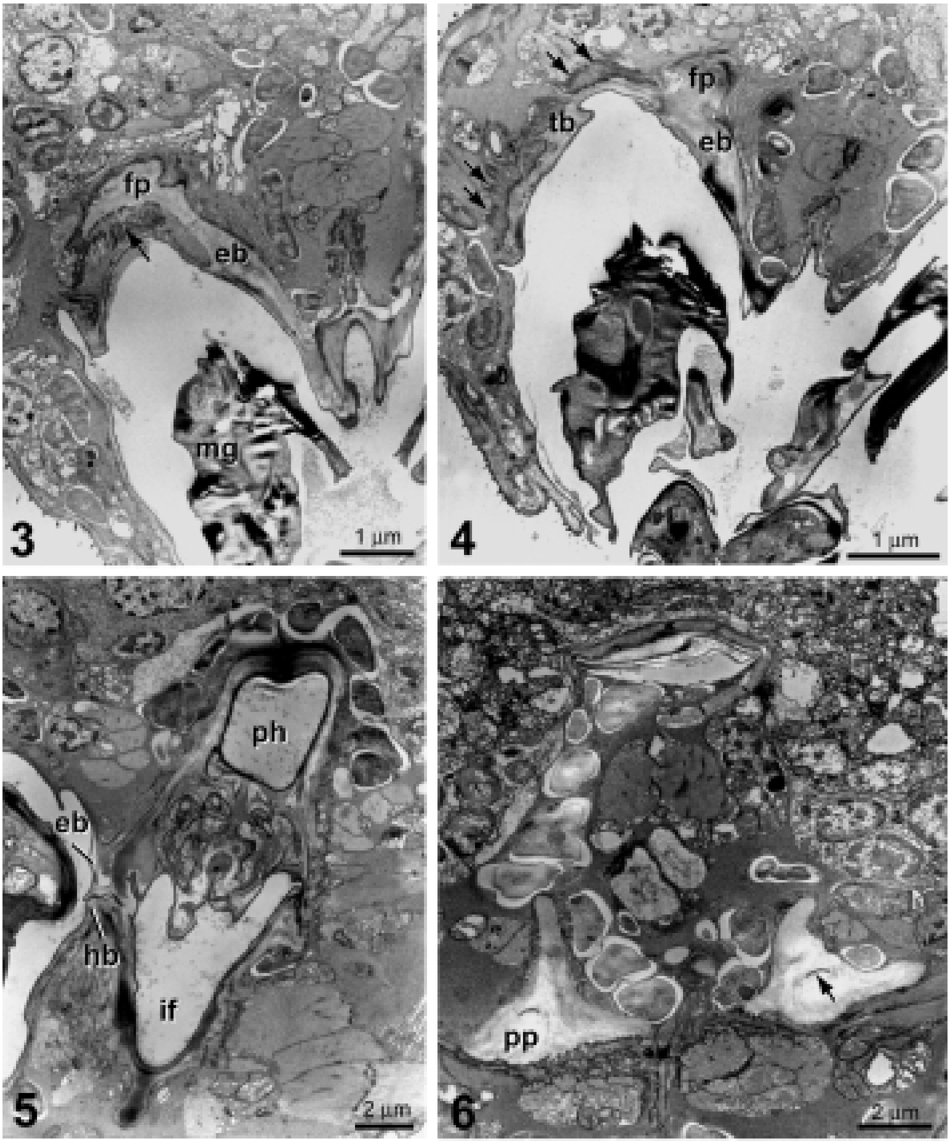


Figs 1–2. Schematic illustration of the cephalic tentorium in (1) *Pauropus* sp. (ventral view) and (2) *Polyxenus lagurus* (dorsal view). Numbered broken lines refer to oblique transverse sections. Abbreviations: *eb* epipharyngeal bar, *fp* frontal process, *hb* hypopharyngeal bar, *pp* posterior process, *tb* transverse bar.

posteriorly within the cephalic lumen. The cuticular nature of these apodemes is evident from the presence of a slit-like cavity lined with exocuticle (Fig. 6) that communicates with the preoral chamber. Differences concern (i) the peculiarity that the anteriormost parts of the apodemes are interconnected by the cuticle of a short, blindly ending pouch (‘infrabuccal chamber’; Fig. 5: *if*) that passes beneath the pharynx into the cephalic lumen. Strikingly, the apodemes are also connected along this pouch with the cuticle of the pharynx. The remaining part of the apodemes differs (ii) in length: they are strongly elongated, extending up to the first trunk segment (collum), and (iii) in showing short lateral branches. Similarly, as in the Lithiobiomorpha, the base of the apodemes pass over into diverging sclerotised bars covering the epi- as well as the hypopharynx. Differences are as follows: The epipharyngeal bars (Figs 3–5: *eb*) converge anteriorly and fuse in the midline of the epipharynx. From the paired components of these bars, an exoskeletal bar diverges laterally. This transverse bar (Fig. 4: *tb*) extends downwards along a fold of the head capsule that encloses the mandibles; differing from the state in Lithobiomorpha, the bar fades out on the inner face of the cephalic fold, with its apex being remote from the margin of the head capsule. Near the base of the transverse bar, another endoskeletal process is formed. This frontal process (Figs 3–4: *fp*) passes into the cephalic cavity as a massive, hook-like apodeme. Both to the frontal process as well as the transverse bar, several muscles are attached, arising from the clypeus and lateral fold of the head capsule. Differing from the state in the Lithobiomorpha, there is no articulation between the epipharyngeal bar and the mandibular gnathal lobe. Instead, articular support for the mandibular gnathal lobe is provided by the hypopharyngeal bar.

Polyxenus lagurus

The structure of the tentorial complex of *Polyxenus lagurus* (Fig. 2) corresponds to the state in chilognathan millipedes as described by Fechter (1961) and Manton (1964). There is no principle difference, but due to the opisthognathous head posture the complex is somewhat rotated such that the posterior processes extend upwards in a nearly vertical plane, while the epi- and hypopharyngeal bars are curved



Figs 3–6. *Pauropus* sp., series of ultrathin transverse sections through the head, showing components of the tentorial complex from anterior to posterior as indicated in Fig. 1. 3. Preoral chamber cut at level of mandibular gnathal lobe (*mg*), showing epipharnygeal bar (*eb*) and frontal process (*fp*). Arrow indicates insertion of muscle fibres. 4. Same, a little farther back, showing transverse bar (*tb*) as a side branch of the epipharyngeal bar (*eb*). Arrows indicate muscle attachments. 5. Same, farther back, showing the base of the right posterior process and its connection to epi- (*eb*) and hypopharnygeal bar (*hb*) as well as pharynx (*ph*) and infrabuccal chamber (*if*). 6. Cephalic cavity, showing posterior processes (*pp*) below the gut. Arrow indicates the cavity of the left posterior process.

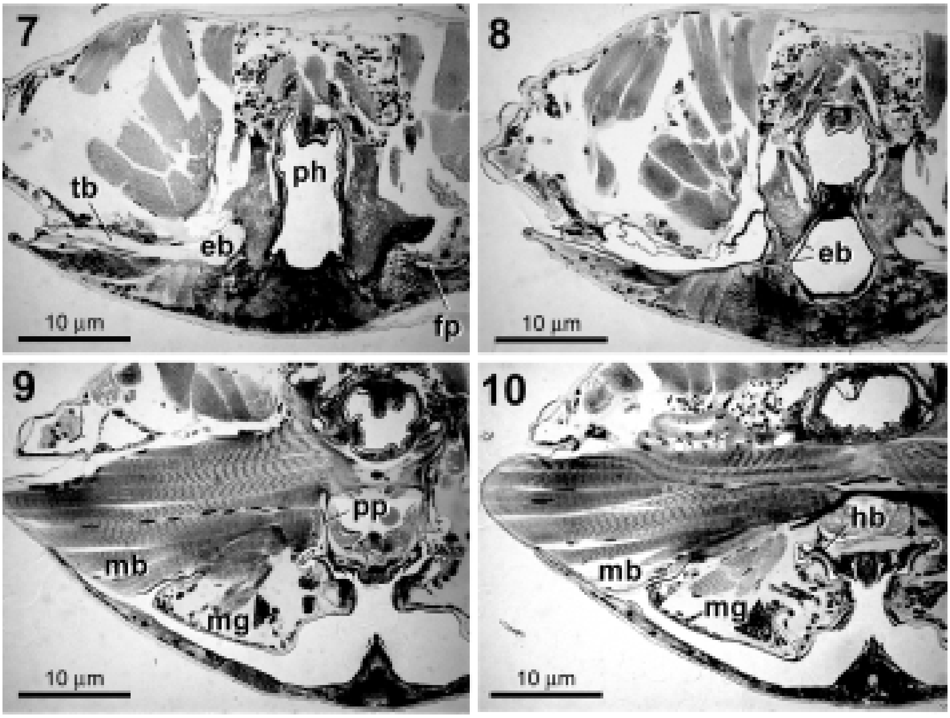
backwards. The posterior processes form short wings rather than being rod-like as in Lithobiomorpha. Their cuticular nature is indicated by the presence of a narrow cavity lined with exocuticle (Fig. 9). The exoskeletal components differ from the state in the Lithobiomorpha mainly in that the epipharyngeal bar is much shorter. Its transverse bar (Fig. 7: *tb*) reaches the margin of the clypeus. As in *Lithobius*, but different from the state in *Pauropus*, the transverse bar projects into the cephalic cavity as a ridge. This ridge serves as an attachment site for several short muscles that arise from the clypeus (Figs 7–8). Laterally, the ridge is connected with an inconspicuous notch in the head capsule. In its position, this notch corresponds to the more prominent 'clypeal notch' (Manton 1964) in the Chilognatha, but it differs from it in being arranged in a nearly horizontal plane. Medially, the ridge forms a short, massive internal process (Fig. 7: *fp*). At this process, a long muscle is attached that arises from the lateral margin of the clypeus. As in *Pauropus*, the mandibular gnathal lobe articulates with the hyopopharyngeal bar only (Fig. 10).

DISCUSSION

Any objections against the monophyly of the Myriapoda would presently be obsolete if the Pancrustacea (Crustacea + Hexapoda) form a monophyletic group: there is no competing hypothesis of relationship for the myriapod subgroups Chilopoda and Progoneata (Edgecombe & Giribet 2002). Under the Tracheata hypothesis ('Myriapoda' + Hexapoda), however, the possibility still cannot be excluded that the Progoneata (Symphyla + Pauropoda + Diplopoda) are more closely related to the Hexapoda than to the Chilopoda (Labiophora hypothesis, e.g. Kraus 2001). The tentorial complex plays a crucial role in this debate, particularly for two reasons:

(i) Its posterior processes may be homologous with the anterior tentorial apodemes in hexapods (see e.g. Manton 1964; Koch 2000; Bitsch & Bitsch 2002). For their apparent absence in crustaceans, these apodemes are accordingly considered to be 'among the most noteworthy potential myriapod/hexapod synapomorphies' (Klass & Kristensen 2001: 272), i.e. their presence *a priori* contradicts the current view that insects are terrestrial crustaceans.

(ii) Swinging movements of the tentorial complex have been proven to form an essential part of the mandible mechanism in Chilopoda (except Scutigeromorpha and Geophilomorpha), Symphyla and Chilognatha (Diplopoda) (e.g. Fechter 1961; Manton 1964; Ravoux 1975). This correlates with the peculiarity that the mandibular gnathal lobe is moveably separated from the mandibular base in these instances. Adduction of the gnathal lobes is based on a mandibular muscle that is directly attached to the gnathal lobe. The homologous muscle in insects and crustaceans, in contrast, is commonly believed to insert on the margin of the mandibular base and to effect the antagonistic movement (abduction). In the myriapods under consideration, this movement is effected or at least enhanced by the tentorial swing. This action is transferred to the mandibular gnathal lobe by its articulation with the exoskeletal components of the tentorial complex, the 'fulturae' *sensu* Snodgrass (e.g. 1952). He claimed that corresponding sclerites are absent in crustaceans and insects. All this appears to form a strong character complex in support of myriapod monophyly (Boudreaux 1979; Kluge 1999; Edgecombe & Giribet 2002).



Figs 7–10. *Polyxenus lagurus*, series of semithin transverse sections through the head, showing components of the tentorial complex from anterior to posterior as indicated in Fig. 2. 7. Head cut in front of oral opening, showing left frontal process (*fp*) and right transverse bar (*tb*) in connection with epipharyngeal bar (*eb*) next to pharynx (*ph*). 8. Same, a little farther back, showing parts of curved epipharyngeal bar (*eb*). 9. Same, farther back, showing mandibular base (*mb*) and gnathal lobe (*mg*) within the preoral chamber and the origin of mandibular muscles from the posterior process (*pp*). 10. Same, a little farther back, showing articulation of mandibular gnathal lobe (*mg*) with hypopharyngeal bar (*hb*).

The reliability of these arguments, however, remain uncertain as available data on the structure of the tentorial complex in myriapods were considered insufficient for final decisions on homology (Kristensen 1998; Edgecombe & Giribet 2002). Missing data especially concern the Hexamerocerata (Pauropoda); apart from a few details on the head morphology provided by Hüther (1968), available data on this group are restricted to taxonomic descriptions. Present knowledge of the state in the remaining pauropod subgroup Tetramerocerata goes back to the work by Silverstri (1902 *fide* Verhoeff 1934) and Tiegs (1947). Likewise, detailed accounts on the head endoskeleton in the Diplopoda are restricted to representatives of the Chilognatha (e.g. Fechter 1961; Manton 1964; Wilson 2002); information on the basal subgroup Pselaphognatha (= Penicillata), in contrast, is still fragmentary (Manton 1961; Kane 1981). Homology estimations were further hampered, partly by the use of different terminologies (Table 1), and partly by the lack of clear distinctions between cuticular and ligamentous (= collagenous) as well as endo- and exoskeletal formations. The present study contributes towards filling in these gaps.

TABLE 1.

Terminology for the components of the myriapod cephalic tentorium in previous descriptions and the present study.

SNODGRASS (1950)	**MANTON (1964)**	**RAVOUX (1975)**	**Present Study**
[illustrated, but not designated]	hypopharyngeal process	apophyse hypopharyngienne (a) = bras oral	hypopharyngeal bar
fulturae [incl. hypopharyngeal arm]	transverse process	apophyse transverse (b) = bras mandibulo-épipharyngien	transverse bar
[epipharyngeal arm]	anterior process	sclerite incurvé	epipharyngeal bar
–	–	[tendon de muscles suspenseurs apophysaires antérieurs]	frontal process
head apodemes	posterior process	apophyse tentoriale (c)	posterior process

The tentorial complex: common pattern

Results obtained support the view that the formations called tentorial in myriapods are homologous. This is especially indicated by the correspondence in position, composition and arrangement of the components (Figs 11–15). In order to describe these components, the use of the terms ‘fulturae’ or ‘fultural sclerites’ proved to be inappropriate. Their composite nature was already recognised by Snodgrass (1950: 52): he distinguished between ‘…the epipharyngeal arm (…) and the hypopharyngeal arm of the corresponding premandibular sternal sclerite of the head [= fulturae] that supports the hypopharynx’ (Fig. 11). Present descriptions of the fultura *sensu* Snodgrass (e.g. Bitsch & Bitsch 2002; Edgecombe & Giribet 2002), in contrast, refer only to a single plate. Accordingly, a new terminology is introduced that is based strictly on topology. It differs from Manton’s (1964) terminology, mainly in that exoskeletal structures are assigned as ‘bars’ rather then ‘processes’; the latter is used for endoskeletal formations only.

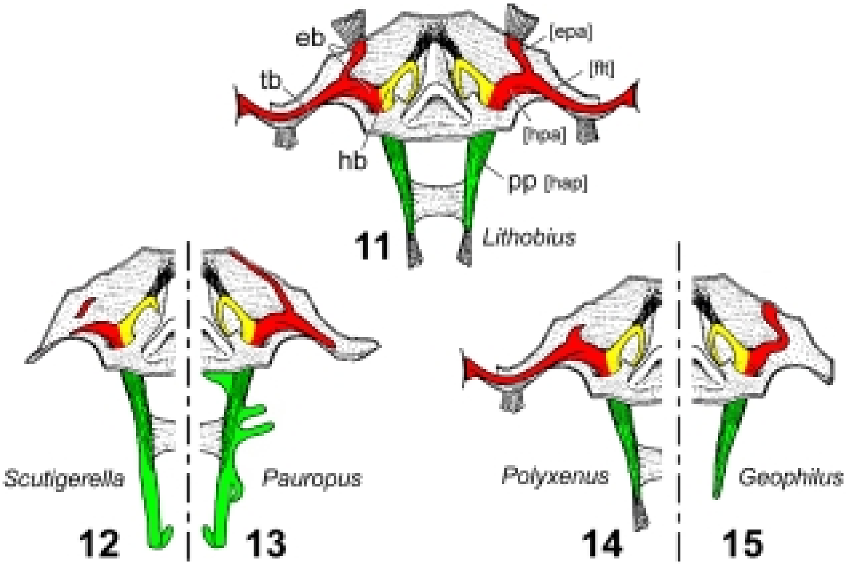
(i) In accordance with previous observations on cephalogenesis (Tiegs 1947), the posterior processes (*pp*) proved to be cuticular ingrowths in the Tetramerocerata (Pauropoda), and also in the Pselaphognatha (Diplopoda). In these subgroups, the apodemes postembryonically show the same point of origin as in the Chilopoda, Symphyla and Chilognatha (Diplopoda): they arise within the preoral chamber just lateral to the oral opening, in that area in which epi- and hypopharyngeal bar pass over into each other. Differences in shape and extension coincide with differences in the extent of muscles originating from these apodemes, as summarised by Bitsch & Bitsch (2002). Short rods as present in the Chilopoda probably constitute the most primitive state of the posterior processes (see below - Problems connected with outgroup comparisons).

(ii) The epipharyngeal bar (*eb*) is generally omitted in recent descriptions of the ‘fulturae’ (e.g. Kluge 1999; Bitsch & Bitsch 2002; Edgecombe & Giribet 2002). In all subgroups of the Chilopoda, it is this bar that is essential for the abduction of the mandibular gnathal lobe: its articulation with this bar by means of a condyle situated at the level of the mandibular molar plate (or its derivative, respectively; see Edgecombe *et al.* 2003) forces the gnathal lobe to open when the mandibular base is protracted—irrespective of whether the tentorial complex is mobile (Lithobiomorpha, Craterostigmomorpha, Scolopendromorpha) or immobile (Scutigeromorpha and Geophilomorpha) (Manton 1965; Desbalmes 1992). A similar articulation forms part of the mandible mechanism in the Symphyla (Ravoux 1975). The sclerite providing articular support for the mandibular gnathal lobe, however, lies isolated within the epipharyngeal wall (Fig. 12). Nevertheless, topographic and functional correspondence permits consideration of this sclerite as a remnant or derivative of the epipharyngeal bar that has lost its connection to the remaining tentorial complex. Differences in the Pauropoda and Diplopoda (Figs 13–14) seem to be modifications correlated with the absence of a corresponding articulation. The lack of this articulation seems plausible as a derived feature that coincides with the coupling of the mandible movements with those of the lower lip (intermaxillary plate or gnathochilarium, respectively), but this peculiarity has been shown only for representatives of the Chilognatha (e.g. Fechter 1961; Manton 1964). Details of the mandible mechanism in the Pauropoda and Pselaphognatha remain to be worked out. At least, an articulation with the hypopharyngeal bar is involved.

(iii) The hypopharyngeal bar (*hb*) shows little structural difference in the myriapod subgroups. In the Chilognatha (Diplopoda), it is used for translating the tentorial swing into the abduction movement of the mandibular gnathal lobe. Manton (1964: 89) regards this as a principle difference to the state in the Chilopoda; in this group, it is the epipharyngeal bar ('anterior process') that mainly serves this purpose. According to her description, however, an articulation between the mandibular gnathal lobe and the hypopharynx is also present and provided with a mobile tentorial complex in chilopods. The articulation point differs only slightly, apparently being situated on an extra bar ('mandibular process') connected with (or even formed by?) the hypopharyngeal bar. The function of the less pronounced hypoharyngeal bar in the Symphyla has never been addressed in previous studies and, hence, remains unclear. The same is true for the Pauropoda and Pselaphognatha (Diplopoda). For the absence of any articulation with the epipharyngeal bar, however, it seems likely that at least in *Pauropus* and *Polyxenus* the translation of the tentorial swing into mandibular movements corresponds to the state in the Chilognatha. This is especially indicated by the presence of a well-developed transverse bar.

(iv) The mobility of the tentorial complex in the Chilopoda and Chilognatha (Diplopoda) is primarily based on the presence of the transverse bar (*tb*): due to its attachment to the 'pleural sclerite' (Chilopoda) resp. 'clypeal notch' (Chilognatha) of the head capsule, it defines the axis about which the tentorial complex performs swinging movements; at once, it provides the main attachment site for the muscles effecting the forward swing—their antagonists, in contrast, mainly insert on the posterior processes (Manton 1964). The muscular equipment of the transverse bar in *Pauropus* and *Polyxenus* indicates that the tentorial complex in these groups is also a mobile formation. Concerning *Pauropus* (Tetramerocerata), this is especially surprising as the mandibular gnathal lobe, different from the state in the Hexamerocerata, is no longer moveably separated, but fused with the mandibular base. Within the Chilopoda, the same is true for the Geophilomorpha (Manton 1965). These differ from the state in *Pauropus*, however, in that the fusion of the mandibular gnathal lobe and base coincide with the loss of the transverse bar (Fig. 15), which leaves the remaining tentorial complex immobile in this group (there may be exceptions; see Snodgrass 1950: Fig. 18G). The missing connection between the lateral apex of the transverse bar and the margin of the head capsule in *Pauropus* hardly contradicts the view that the tentorial complex is mobile, as a connection of this kind is also missing in the Symphyla (Fig. 12). In this group, the transverse bar is even much shorter; its muscular equipment is accordingly more simple, with all muscles being attached at a massive cuticular tendon of the transverse bar (Ravoux 1975). Topographic correspondence supports a homology between this tendon and the frontal process (*fp*) in *Pauropus* and *Polyxenus*. For the apparent absence of this tendon in the Chilopoda (albeit indicated by Applegarth 1952: Fig. 82B) and Chilognatha (Diplopoda), however, it remains questionable whether the frontal process belongs to the ground pattern of the tentorial complex in myriapods.

The homology of the tentorial complex in myriapods may accordingly be further reasoned by the presence of a corresponding set of muscles providing the tentorial mobility by their attachment to the transverse bar. The ground pattern and also the origin of this muscular set, however, remain to be clarified.



Figs 11–15. Frontal view of tentorial complex in 11. *Lithobius* (Chilopoda) as illustrated by Snodgrass (1950, modified) and corresponding components, drawn on the same illustration for direct comparison, in 12. Symphyla, 13. Tetramerocerata (Pauropoda), 14. Pselaphognatha (Diplopoda) as well as 15. Geophilomorpha (Chilopoda). Abbreviations (in brackets: Snodgrass's terminology): *eb* epipharyngeal bar, *epa* epipharyngeal arm, *flt* fultura, *hap* head apodeme, *hb* hypopharyngeal bar, *hpa* hypopharyngeal arm, *pp* posterior process, *tb* transverse bar.

‘Positive’ characters in favour of the Myriapoda?

In order to establish Myriapoda as a clade, arguments that relate to the tentorial complex were detailed as follows (Kluge 1999; Edgecombe & Giribet 2002): (i) presence of ‘fulturae’ that support the hypopharynx, with a specific arrangement relative to hypopharynx and head apodemes, (ii) bipartite mandible: mandibular gnathal lobe moveably separated from its base, (iii) mandibular gnathal lobe musculated, its flexor being derived from the anterior dorsal muscle of the extrinsic leg musculature, (iv) posterior dorsal muscle of the mandible lost, (v) mandibular gnathal lobe articulated to the fulturae, (vi) abduction of the mandibular gnathal lobe based on swinging movements of the tentorium.

There are two main reasons why these arguments have never found general acceptance:

1. *Problems connected with outgroup comparisons*

Insufficient descriptions of the character states in crustaceans still render homology estimations difficult. Yet, components of the myriapod tentorial complex have been identified only in hexapods. Recent findings (Koch 2000) support previous assumptions (e.g. Snodgrass 1950, Manton 1964) that the anterior tentorial apodemes in hexapods, primarily short rods as in the Chilopoda, are homologous with the posterior processes of the tentorial complex in myriapods (Bitsch & Bitsch 2002). The same even seems to be true for slender exoskeletal branches of the epi- and hypopharynx that in the Collembola (Hexapoda) converge to the point of origin of the anterior tentorial apodemes (Koch 2000). Thereby, a similar tentorial complex is formed as present in the Geophilomorpha (Chilopoda), deviating from the common pattern as employed in this study, mainly in that the transverse bar (muscles and frontal process included) is absent (Fig. 15). A tentorial complex of this kind is missing in the remaining hexapod subgroups, but their components are presumed to be still present in the Ectognatha: the so-called oral arms of the hypopharynx and sclerotised bars bordering the epipharynx (see Koch 2000 2001). In contrast, paired exoskeletal rods assigned as ‘fulturae’ in hexapods (e.g. Bitsch & Bitsch 2000) proved to show quite a different position than the fulturae in myriapods (Koch 2000; Bitsch & Bitsch 2002): extending along a groove between the arthrodial ‘membranes’ (i.e. elastic, non-sclerotised cuticle) of first and second maxillae, they connect the hypopharynx with the posterior tentorial apodemes. Comparable formations are absent in myriapods. Concerning Crustacea, uncertainties remain upon whether components of the tentorial complex are generally absent. At least in Isopoda (Marvillet 1978) and Stomatopoda (Kunze 1981), endoskeletal formations occur that recall the anterior tentorial apodemes in hexapods and myriapods. Their topographic correspondence, however, remains to be clarified.

Persisting uncertainty also concerns the derivation of the mandibular muscles in myriapods. Kluge (1999) as well as Edgecombe & Giribet (2002) followed Boudreaux’s view (1979), which itself was based on Manton’s (1964) interpretation. Her reason for considering the flexor of the mandibular gnathal lobe in myriapods as a derivative of the formerly anterior dorsal muscle, simply refers to the fact that the cuticular tendon on which the flexor inserts passes backwards (towards the dorsal cranial wall) *above* the ligamentous transverse mandibular tendon. The same is true for the cuticular tendon in hexapods and crustaceans (if present) that the abductor muscles insert on. In contrast, the derivatives of the posterior dorsal muscle, also arising from the dorsal cranial wall, are attached at a cuticular tendon that extends *below* (or behind) the transverse mandibular tendon. This different arrangement, however, hardly justifies excluding the alternative view that the posterior rather than the anterior dorsal muscle was transformed into the flexor of the gnathal lobe. The alternative seems to be even more probable as the derivatives of the anterior dorsal muscles in hexapods are primarily attached directly at the mandibular base; within the Hexapoda, their insertion on a tendon formed by the anterior margin of the mandibular orifice is found only in the Dicondylia (Zygentoma + Pterygota) and, hence, seems to be a derived state (Koch 2001). Accordingly, only one cuticular tendon of the mandibular base probably belongs to the hexapod ground pattern: the one on which the posterior dorsal muscle inserts. The alternative view is also in accordance with the presence of cranio-mandibular muscles in myriapods that still are attached at the anterior margin of the mandibular orifice (e.g. Snodgrass 1950: muscle 2A). Considering the posterior dorsal muscle to be shifted towards the gnathal lobe, hence, provides a more simple explanation without the need to infer any loss of muscles. Manton's (1964) view, in contrast, implies not only the loss of the posterior dorsal muscle, but also the fragmentation of the anterior dorsal muscle and the gain of a cuticular tendon as attachment site for the anteriormost fragments.

Albeit plausible, there is, however, no evidence at all that the flexor of the gnathal lobe is derived from the extrinsic leg musculature. According to the current view that the mandibular gnathal lobe in crustaceans evolved from a mobile proximal endite (e.g. Walossek 1999), the possibility cannot be excluded that the flexor of the gnathal lobe in myriapods rather corresponds to an enditic muscle (Koch 2001). Although this view deserves further attention, there is at present no sufficient reason for the underlying assumption that the mandibular gnathal lobe in myriapods and hexapods is also derived from a formerly small mobile endite.

Hence, of the explanations for the evolutionary process leading to the flexor of the mandibular gnathal lobe in myriapods, it is the derivation from the formerly posterior dorsal muscle that presently seems to be the most parsimonious assumption. Common markers to identify homologous muscles, origin and insertion, however, fail to exclude alternative hypotheses in this instance. The same is true for the innervation of the muscles as relevant data is generally missing. The homology of the mandibular muscles accordingly needs further consideration.

2. *Controversial views on mandible evolution*

The characters of concern all relate to the peculiarity that the mandibular gnathal lobe in myriapods is moveably separated from the mandible base. The presence of a muscle pulling directly on the gnathal lobe represents the most efficient solution for strong biting (adduction), but this implies its separation from the mandibular base. For mastication, a moveably separated mandibular gnathal lobe relies on an efficient indirect abduction mechanism: the 'swinging tentorium'. The mobility of the tentorium primarily relies on the presence of 'fulturae', its transverse component (= transverse bar) in particular. Finally, translation of the tentorial swing into mandibular movements relies on the articulation between mandibular gnathal lobe and tentorium. Although this character complex is indeed unique, it is still repeatedly ignored as a potential myriapod synapomorphy. This is mainly due to claims that the mandibular gnathal lobe in hexapods is secondarily fused with the mandible base (e.g. Kraus 1998 2001; Kukalová-Peck

1998; for review, see Bitsch 2001), as in the Geophilomorpha (Chilopoda) and Tetramerocerata (Pauropoda). Evidence for the gnathobasic nature of myriapod and hexapod mandibles (Popadic *et al.* 1998; Scholtz *et al.* 1998) hardly excludes this possibility. Yet, this view was based only on the presence of structural borders (internal ridges or sutures) within the single-piece mandible of primarily wingless hexapods, especially Archaeognatha. These borders allegedly correspond in position to the joints between the (primarily) three components (cardo, stipes, gnathal lobe) of the mandibles in the Diplopoda. Embryological observations (Machida 1996, and personal communication, but not mentioned in 2000) confirmed the presence of two components within the mandibular base in the Archaeognatha. Its muscular equipment (see e.g., Koch 2001), in contrast, contradicts the view that these components correspond to cardo and stipes of diplopod mandibles. Further arguments against their correspondence concern (i) the exceptional presence of similar 'borders' within the mandibular base in the Stomatopoda (Crustacea); they proved to be significant in function only (Koch 2002); (ii) in myriapods, the presence of a bipartite mandibular base is restricted to the Hexamerocerata (Pauropoda) and Diplopoda (Pselaphognatha included; Kraus, personal communication) and, hence, rather seems to be a derived state of the Dignatha (Pauropoda + Diplopoda). This is in accordance with the view that the fragmentation of the mandible in the Chilopoda concerns the gnathal lobe only; the mandibular base, strongly narrowed, forms a single piece (Desbalmes 1992), as in the Symphyla. A secondary subdivision of the mandibular base in the Dignatha seems to be plausible for the peculiarity that the mandibles are used not only for mastication, but also for hauling food into the preoral chamber (Kraus & Kraus 1994). As far as known (Hexamerocerata?), there are no longer any other mouthparts that could serve for this purpose. A subdivision of the mandibular base would accordingly be advantageous for providing a wider radius to the gnathal lobes. All this favours the view that myriapod mandibles are primarily bipartite only: composed of mandibular base and gnathal lobe (Kluge 1999).

Recent insights on the mandible mechanism in primarily wingless hexapods (Koch 2001), however, provide further support for the view that the mandibular gnathal lobe is secondarily fused with the mandible base. This is not only due to the presence of a tentorial complex in the Collembola that resembles that in the Geophilomorpha (Chilopoda). In the Collembola and Diplura, the mandibles also show a similar abduction mode: for the absence of any mandibular muscle that could serve for this purpose, the abduction of the gnathal lobe is based on the protraction of the mandible; this movement is guided by the (non-permanent) articulation of the gnathal lobe with the epipharyngeal bar of the tentorial complex, which forces the gnathal lobe to open. An articulation of this kind (Koch 2001: 'clypeal articulation') proved to be present also in the Zygentoma and Ephemeroptera (Pterygota), in addition to another non-permanent articulation (ibid.: 'tentorial articulation') that fixes the axis of the mandibular movement. 'Tricondylic' mandibles were accordingly considered to belong to the ground pattern of the Hexapoda. This view was subsequently criticised for not taking into account that Collembola and Diplura show derived states correlated with entognathy (Bitsch 2001). This may even be true; the possibility, however, that entognathy—i.e. presence of cranial folds overhanging the mandibles—is a primitive state in myriapods and hexapods (Lauterbach, personal communication) requires reconsideration.

Other characters in support of myriapod monophyly?

Another argument derived from the morphology of the mandibles was recently introduced by Edgecombe & Giribet (2002): presence of pectinate lamellae on the mandibular gnathal lobe. The overall similarity in the Chilopoda and Diplopoda clearly suggests homology. Considering these microstructures as a myriapod synapomorphy, however, suffers from the fact that they are absent in the Symphyla and are undocumented in the Pauropoda. Also, they may not be as unique as indicated: similar rows of 'comb-like bristles' frequently occur in stream-living insects that feed on algae (Arens 1994), but these are not formed on the mandibular gnathal lobe, but on the endites of first or second maxillae. Their distribution indicates that they were acquired independently several times in insects on those mouthparts that are used for hauling and transferring food particles towards the mouth. In Chilopoda and Diplopoda, this function is mainly taken over by the mandibles; both pairs of maxillae, if present, no longer serve this purpose, which partly coincides with the loss of the corresponding endites (see Borucki 1996). In the Symphyla, in contrast, the morphology of the first maxillae suggests that a functional cooperation with the mandibles—as commonly found in insects and crustaceans—is maintained (see e.g. Ravoux 1975; Kraus & Kraus 1994). This favours the view that the restriction of these functions (hauling and transport of food particles in addition to mastication) to the mandibles is a derived state, independently acquired in the Chilopoda and Diplopoda (but see Kraus & Kraus 1994: 15); the same would accordingly be true for the gain of pectinate lamellae. However, further studies should clarify whether the comb-like bristles in insects and the pectinate lamellae in myriapods are comparable formations.

Remaining arguments derived from morphology were recently revised by Edgecombe & Giribet (2002); for detailed discussion, the reader is referred to this review. Based on the available data, their phylogenetic value is also difficult to assess at present. Primarily, they concern 'absence characters' related to sense organs (eyes and scolopidia) and the structure of the spermatozoa. Under the Tracheata hypothesis (= 'Myriapoda' + Hexapoda), these are interpreted as reductive traits; as such, their phylogenetic significance was considered to be highly questionable (see Dohle 1998 *versus* Ax 2000). The same, however, is true under the Pancrustacea hypothesis (Crustacea + Hexapoda): it is no longer possible to exclude the absence of these characters being plesiomorphic. Further implications concern characters related to terrestrial life habits that myriapods share with hexapods (see Ax 2000: 203). They remain as potential synapomorphies of the Myriapoda under the assumption that the Hexapoda form the sister group (or a subgroup) of the Crustacea. However, if these characters are prone to have resulted from convergent evolution in hexapods despite general correspondences with the state in myriapods, they can hardly be accepted as strong support for the monophyly of the Myriapoda.

CONCLUSIONS: WHY NOT ACCEPT MYRIAPODA AS A CLADE?

A considerable number of arguments derived from comparative morphology potentially support the monophyly of the Myriapoda, but none of them can presently be considered as unambiguous. The most convincing potential synapomorphy of the Myriapoda still refers to the mandible morphology and mechanism: the abduction of a primarily moveably separated gnathal lobe by means of a 'swinging tentorium' is not found in any other mandibulate arthropod. Present evidence for the homology of the tentorium in myriapods, however, strengthens the hypothesis that homologous components of the tentorium are also present in hexapods: the anterior tentorial apodemes and the associated exoskeletal epi- and hypopharyngeal bars. These components represent potential synapomorphies of myriapods and hexapods in as much as comparable formations have not yet been pointed out for any crustacean. The synapomorphic state in myriapods has accordingly to be specified: presence of an additional component, the transverse bar, which provides tentorial mobility due to its apparently unique muscular equipment; and perhaps the fact that all components primarily form a functional and structural unit in myriapods, while in hexapods this can be stated with certainty only for a unit composed of epipharyngeal bar and anterior tentorial apodeme. The cuticular cephalic endoskeleton provides no further indication that any myriapod subgroup is more closely related to hexapods than to the remaining myriapod subgroups. Available data on the tentorial complex rather favour myriapod monophyly, even under the Tracheata hypothesis.

Objections against the view that the tentorial mobility is a myriapod synapomorphy result from corresponding character states in Geophilomorpha (Chilopoda) and basal hexapod subgroups formerly united as ‘Entognatha’. In particular, the presence of a corresponding tentorial complex in the Collembola supports the previous assumption that the mandibular gnathal lobe in hexapods is secondarily fused with the mandible base. Under the Tracheata hypothesis, this view remains a reasonable assumption, but it still suffers from being derived solely by analogy; convergence in correlation with entognathy cannot be excluded. For final decisions with regard to the Pancrustacea hypothesis, the homology not only of the mandibular muscles in myriapods requires clarification. The origin of the muscles that effect the tentorial swing also remains enigmatic; no homologues have yet been identified in crustaceans and hexapods. Their attachment at components of the tentorium that are considered to be remnants of the premandibular (= tritocephalic) sternite (e.g. Snodgrass 1950) suggests that these muscles may be derived from the extrinsic musculature of the tritocephalic appendages (= second antennae in crustaceans). Accordingly, for its potential to explain the absence of these appendages not only in myriapods, but also in hexapods, the tentorial complex deserves further attention.

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